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INHERITANCE OF HABIT IN THE COMMON BEAN

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HABIT is the external form of a plant taken as a whole. It is usually described by a few general adjectives, such as erect, open, spreading, etc. However, to study the inheritance of plant habit, a detailed analysis of the real characters underlying habit must be made. It is usually found that the general outer appearance of a plant, its habit, is the result of a combination of independent characters, units, the recombination of which by crossing often results in plants much altered in appearance from the parent varieties. Characters usually unimportant may be found of primary importance in the formation of plant habit.

An example of such inheritance of habit is found in one of Webber's pepper hybrids (6). A cross was made between Red Chili, a variety with many erect fine branches, and Golden Dawn, with few, horizontal, coarse branches, both being of medium size. In the second generation recombination and segregation of the three character pairs occurred, although not in strict Mendelian proportions. The important feature of the results, however, lies in the apparent creation of a giant and a dwarf type, not by the appearance of new units by mutation, but simply by the transference of the characters fine and coarse branches. Hybrids having erect, many and coarse branches were giants, while those having few, horizontal and coarse branches were dwarfs. Other combinations of these characters gave intermediate forms.

The study here reported was made largely on third and fourth generation plants and a few second generation plants of hybrids made primarily for the study of pig-

mentation. The material worked with, owing chiefly to lack of knowledge of earlier generations, offered many limitations and is unsuited to a detailed analysis of the characters in question. As the plants were usually not more than six inches apart in the rows, the crowding in the later stages of development hindered accurate judgment of the habit type.

With reference to general habit bean plants are either pole or bush. Pole beans are commonly long twining vines, climbing when provided with poles or other support. The true bush type is usually short, erect and non-twining. There are also certain races of beans really intermediate between the true bush and pole types, the runner beans, which are non-climbing. Types classed as bush beans also occur, which are spreading and possess outstretched branches of a more or less runner-like character.

The following table contains a description of habit of varieties of beans considered in this discussion. The descriptions are from "American Varieties of Garden Beans" (5). The varieties observed agree with these descriptions except in the case of Mohawk, which is described as without runners. The strain of Mohawk isolated here produces runners.

TABLE I

DESCRIPTION OF BEAN VARIETIES

Pole Beans ALT¹

Golden Carmine—Small, good climber.

Creasback—Small, at first bush-like, poor climber when young.

Runner Beans ALt

White Marrow—Very large, very spreading, many runners.

Bush Beans ALT

Burpee Stringless—Large, medium, very erect when young, with a few shoots high above the plant, but more or less spreading when mature; no runners.

Giant Stringless—Same as above.

¹ For the meaning of these letters see page 550.

Semi-runner Forms Alt

Refugee—Very large, very spreading, many semi-runners.

Refugee Wax—Large, medium, very spreading, many runner-like branches.

Spreading Forms aLT or aLt

Longfellow—Large to medium, somewhat spreading, many outstretched branches, no real runners.

Kenny Rustless—Large, very spreading, almost runner-like branches.

Prolific Black Wax—Medium, more or less spreading, sometimes long outstretched branches, no real runners.

Erect Forms alT or alt

Black Valentine—Large, medium, fairly erect, occasional drooping branches, no real runners.

Blue Pod—Medium, erect, no runners or spreading branches.

Bountiful—Large, medium, fairly erect when young, but drooping when mature, no runners or decided spreading branches.

Burpee Kidney—Large, no runners, but usually drooping with fruit-laden branches and spreading when mature.

Burpee White Wax—Large, sometimes with drooping branches, but no real runners.

Challenge Black Wax—Very small, erect, no runners or spreading branches.

Curries—Medium, erect, no runners or spreading branches.

Davis Wax—Large, medium, erect, no runners.

Early Refugee—Medium, very erect, no runners or spreading branches.

German Black Wax—Medium, erect when young, usually borne down with fruit laden branches when mature, no runners.

Long Yellow Six Weeks—Medium, very erect, no runners or spreading branches.

Low Champion—Very large, usually erect, no runners or spreading branches.

Mohawk—Large, very erect, no runners, sometimes drooping when old.

Red Valentine—Medium, erect, no runners or spreading branches.

Round Yellow Six Weeks—Small, medium, very erect, no runners or spreading branches.

Wardwell—Large, medium, fairly erect, no runners.

Warren—Very large, usually erect, no runners or decided spreading branches.

Warwick—Medium, erect, no runners or spreading branches.

R. A. Emerson in his experiments on heredity of plant habit in beans found three main character pairs concerned, namely, length of plant axis, developed in various degrees; twining habit or circumnutation developed in various degrees or not at all; and lastly, the position of pods, axial or terminal. His data involve chiefly the latter character pair, which is inherited in a 3:1 propor-

tion, the axial position of pods being dominant. The position of pods or flowers influences plant habit in this manner: when flowers are formed at the growing tip of a main stem or branch, such a stem or branch must necessarily cease to elongate; on the other hand, if no flowers or fruits are formed at that point it may continue to grow indefinitely.

The habit of all the varieties of beans can be accounted for easily with only these three character pairs. In Table I the varieties here concerned have been grouped according to the probable presence or absence in them of the characters mentioned.

I have designated the axial position of the pods as A, the terminal position by a; long plant axis by L, short by l; a long axis was shown to be dominant over short in some of Mendel's crosses of beans (1). I have designated circumnutation by T and its absence by t, as, judging from Emerson's statements, and according to my own observations twining habit is dominant. The possible combinations of these characters are as follows:

HABIT TYPES

Type *a*, ALT.... Pole beans.

Type *b*, ALt..... Runner beans.

Type *c*, AlT..... Shoots.

Type *d*, Alt..... Semi-runners.

Type *e*, $\left. \begin{array}{l} 1 \text{ aLT} \\ 2 \text{ aLt} \end{array} \right\} \dots\dots \text{Spreading with long outstretched branches.}$

Type *f*, $\left. \begin{array}{l} 1 \text{ alT} \\ 2 \text{ alt} \end{array} \right\} \dots\dots \text{Erect bush beans.}$

Type *a* comprises the pole beans, as the vines are of great length, both on account of long axis and not being checked by any terminal inflorescence, and as they can climb by virtue of circumnutation.

Type *b* comprises the runner beans. They are like the pole beans except that the climbing habit is not developed to any great extent, if at all. Between these two types it is difficult to draw sharp distinction, but the true runner probably lacks the factor for twining.

Type *c* probably represents the varieties which early send up a few shoots high in the air like Burpee Stringless. In such beans the growth of the main stems or branches is not entirely prevented by the absence of the character which produces a long axis, and as the climbing habit is more or less developed, the characteristic shoots are sent up.

Type *d* represents the semi-runners, caused by the short axis.

Combinations of type *e* and *e*₂ are the spreading varieties, with long outstretched branches. They are to be distinguished from runners by terminal inflorescences. Kenny Rustless is a representative of the *e* type of habit and probably Prolific Black Wax also.

The last two combinations, *f* and *f*₂, are the typical erect bush form, such as Blue Pod Butter and Challenge Black Wax.

Table II gives the possible crosses of these types and the F₂ proportions to be expected when the forms crossed are the most nearly typical. In the cases of typical forms, the F₂ types should be differentiated without much difficulty. A circumstance that must be looked upon as a possible cause of exceptions is the presence of unknown factors that cause variations in the intensity of the development of the twining habit and of the intermediate lengths between long and short axis. If there are various factors for length, as Emerson assumes to be the case in all quantitative characters (3), and if the twining habit is to be explained in much the same way, results may be considerably at variance with the expectations indicated in Table II. It must be remembered that the constitutions given for the varieties are only assumed.

At present, owing to circumstances mentioned before,

TABLE II

No.	Constitution	Type	F ₂ Proportions
1	ALT × ALT	<i>a</i> × <i>a</i>	<i>a</i>
2	ALT × ALt	<i>a</i> × <i>b</i>	3 <i>a</i> : 1 <i>b</i>
3	ALT × ALT	<i>a</i> × <i>c</i>	3 <i>a</i> : 1 <i>c</i>
4	ALT × Alt	<i>a</i> × <i>d</i>	

	ALT		7a	
	ALt	gametes	2	3b
	AlT			3c
	Alt			1d
			<hr/> 9a: 3b: 3c: 1d	
5	ALT × aLT	a × e	3a: 1c	
6	ALT × aLt	a × e		
	ALT	gametes	7a	
	ALt		2	3b
	aLT			3e ₁
	aLt			1e ₂
			<hr/> 9a: 3b: 4c	
7	ALT × alT	a × f	7a	
	ALT	gametes	2	3b
	AlT			3e
	aLT			1f
	alT		<hr/> 9a: 3b: 3e: 1f	
8	ALT × alt	a × f	15a	
	ALT		6	7b
	ALt		4	7c
	AlT		2	2 2 3d
	Alt			7e
	aLT			5
	aLt			3f
	alT			1
	alt		<hr/> 27a: 9b: 9c: 3d: 12e: 4f	
9	ALt × ALt	b × b	b	
10	ALt × AlT	b × c	9a: 3b: 3c: 1d as in type No. 4.	
11	ALt × Alt	b × d	3b: 1d	
12	ALt × aLt	b × e	3b: 1e	
13	ALt × aLT	b × e	7a	
	ALT	gametes	2	3b
	ALt			3e
	aLT			1
	aLt		<hr/> 9 3 4	
14	ALt × alT	b × f	27a: 9b: 9c: 3d: 12e: 4f as in type No. 8.	
15	ALt × alt	b × f		
	ALT	gametes	7b	
	AlT		2	3d
	aLT			3e
	alt			1f
			<hr/> 9b: 3d: 3e: 1f	

16	AlT × AlT	$c \times c$	c
17	AlT × Alt	$c \times d$	$3c: 1d$
18	AlT × aLT	$c \times e$	$9a: 3c: 3e: 1f$ as in type No. 7.
19	AlT × aLT	$c \times f$	
20	AlT × aLt	$c \times e$	$3c: 1f$
21	AlT × alt	$c \times f$	$27a: 9b: 9c: 1d: 12e: 4f$ as in type No. 8.
	AlT		$7c$
	Alt		$2 \quad 3d$
	aLT		$3f$
	alt		1
			$9c: 3d: 4f$
22	Alt × Alt	$d \times d$	d
23	Alt × aLT	$d \times e$	$27a: 9b: 9c: 3d: 12e: 4f$ as in type No. 8.
24	Alt × aLt	$d \times e$	
	ALt		$7b$
	Alt		$2 \quad 3d$
	aLT	gametes	$3e$
	alt		$1f$
			$9b: 3d: 3e: 1f$
25	Alt × aLT	$d \times f$	$7c$
	AlT		$2 \quad 3d$
	Alt		$3f$
	aLT	gametes	1
	alt		$9c: 3d: 4f$
26	Alt × alt	$d \times f$	$3d: 1f$
27	aLT × aLT	$e \times e$	e
28	aLT × aLt	$e \times e$	e
29	aLT × aLT	$e \times f$	$3e \times 1f$
30	aLT × alt	$e \times f$	
	aLT		$7e$
	aLt		5
	aLT	gametes	$3f$
	alt		$1f$
			$12e: 4f$
			$3: 1$
31	aLT × aLt	$e \times e$	e
32	aLT × aLT	$e \times f$	$3e: 1f$ as in type 30.
33	aLT × alt	$e \times f$	$3e: 1f$
34	aLT × aLT	$f \times f$	f
35	aLT × alt	$f \times f$	f
36	alt × alt	$f \times f$	f

only general notes on the behavior of various types of crosses can be given.

TYPE 2. ALT \times ALt

In the third generation of a cross of Creasback, a typical pole bean with White Marrow, a runner bean with probably a weak character for circumnutation, all lots were of axillary inflorescence. The habit of climbing was developed in various degrees so that classifications of types was difficult.

CROSS TYPE 6 OR 7. ALT + aLT or aLt

Notes on an early cross of Creasback by Prolific Black Wax indicate that the generation F_1 were pole beans, the generation F_2 segregating into 33 pole and 8 bush. The latter is probably a 3:1 proportion as expected. Whether all plants described as bush were of the spreading type does not appear from our records.

CROSS TYPE 8. ALT \times alt or aLT

In a cross of Creasback with Blue Pod, a typical bush bean, there occurs one strain of homozygous pole plants, and also in the F_4 generation heterozygous types. Pole and runner forms and bush forms of various types occur in the proportions of 9:7 in one lot and in another of 3:1, as might be expected in an F_4 generation. In another small lot occur plants with long outstretched branches, in another two plants of *c* type of habit. Evidently Blue Pod has the constitution alt.

The data from a cross of Creasback with Blue Pod do not signify much, as the types isolated happen to be constant, one a pole type and bush types, of which several are described as somewhat spreading. In one there occurs a runner bean.

Creasback and Warwick crosses in the F_4 generation behave consistently with the cross type, as assumed. In one lot, 12 have axial inflorescence and three terminal. Lots with spreading plants occur and one plant was noted which possessed a very long axis, along with a twining habit, but also terminal inflorescence. According to the

explanation of habit characters assumed, such a plant would have the formula aLT. Without a support which happened to have been placed near it, the peculiarity of the plant would not have been so noticeable.

A cross of Mohawk and Golden Carmine, a pole bean, gave in the F_2 generation 7 plants of the bush type and 28 plants more or less pole like. In the notes no separation of pole and runner beans were made, probably due to a lack of clear distinction between the two as occurs in many crosses.

CROSS TYPE 10. ALt \times ALT

White Marrow by Burpee Stringless is presumably a cross of this type. In one case the F is described as a pole and in another as a runner bean. The F_2 generation results in 38 bush to 108 described as runner beans. This is consistent with expected results when the plant is described as a whole. The expectations are 12 pole and more or less pole like beans and four more or less bush like forms.

CROSS TYPE 12 OR 13. ALt + aLT OR aLt

A cross of White Marrow, a runner variety, with Prolific Black Wax, which belongs to the type with spreading outstretched branches, gave 20 bush plants and 58 plants of the runner and pole types, no differentiation being made between the two. This is consistent with the assumed constitutions.

CROSS TYPE 14 OR 15. ALt \times alt OR aLT

White Marrow with Currie behaves according to expectation, giving in the F_2 generation 41 bush plants *e* or *f* in type, and 52 of the runner or semi-runner type.

In the cross of Blue Pod by White Marrow and its reciprocal, neither variety being pole in type, climbing plants apparently occur as well representative of most if not all of the other habit types. Some lots isolated were very erect, others spreading in various degrees; one lot is de-

scribed as having long tendril-like shoots above the plant, another along side of this had shorter shoots, perhaps ALT. Among the lots, all degrees of climbing were developed; one plant encountered was evidently aLT like the one mentioned in a previously discussed cross; plants with more or less outstretched branches were noted. Type notes on F_1 and F_2 generations of an earlier cross in type; F_2 segregates into 25 bush forms and 62 runners, are significant. The F_1 generation is described as pole probably including pole beans of the F_1 type. The ratio is disturbed by the lack of a clear understanding of the true basis for classification of plant type in beans. The F_2 of another cross involving the same varieties is noted as having 41 bush and 5 runner beans.

White Marrow and Burpee Kidney yielded two lots of bush beans and two heterozygote lots giving 6 plants with terminal inflorescence and 15 with axillary.

Red Valentine and White Marrow crosses give similar results. In an early cross, the F_2 generation plants have been grouped according to the general plant type, no attempt being made to separate intergrading types. The notes give the results of segregations as 75 bush and 136 runner beans. Later generation heterozygotes approach a proportion of 9 runner to 7 bush beans. The apparent behavior probably depends on whether the intermediate types are classed as runner or bush. In the cross in which only the F_4 generation was observed, only constant bush types seem to have been isolated.

CROSS TYPE 19 OR 21. ALT \times alt OR aLT

Blue Pod crossed with Burpee is a representative cross of this type. Only in a few cases was the Burpee type, plants with shoots high in the air, observed, as most lots isolated were homozygous and erect. In the F_2 generation of an early cross, plants described as runners appeared. The proportion was 3 runners to 1 bush. Heterozygote lots descended from these plants segregated in the same manner, totaled 18 bush and 71 so-called run-

ners. The runners are probably really *c* in type or *c* and *d*.

In the cross of Giant Stringless and Blue Pod the parent types were both isolated. No semi-runners were noted, as would be the case if the cross were No. 21 in type.

CROSS TYPE 25 OR 26. $\text{Alt} \times \text{aLT}$ OR alt

Refugee Wax is a semi-runner bean. The F_3 isolated lots of this variety crossed with Blue Pod were all more or less erect. Some lots homozygous for axial branching were isolated, many individuals of which showed signs of climbing. The semi-running and climbing branches were short, confirming the assumption that neither variety used possesses the factor for a long axis. The climbing tendency exhibited shows that there must be strains of Blue Pod that possess T. Previous data are in harmony with this.

CROSS TYPE 29, 30, 34 OR 35. aLT OR $\text{aLt} \times \text{alt}$ OR aLT

Many crosses of bush beans with those of spreading type give a 3:1 proportion in the F_2 and later heterozygous lots.

In Keeny Rustless, a variety of the spreading type, with its almost runner-like branches, by Red Valentine some lots with the spreading habit have been isolated, also more or less runner-like forms and one with the erect habit of Red Valentine. The axial and terminal inflorescence is inherited in a 3:1 proportion. Notes on type in one heterozygous lot show five erect and 10 plants with outstretched branches.

In the cross of Black Valentine and Prolific Black Wax one lot with outstretched branches was isolated; all others were of the erect type.

In the cross of Blue Pod Butter and Prolific Black Wax no spreading types with outstretched branches were noted, but this is not surprising, as in an F_4 generation the parent plants selfed for planting may not have hap-

pened to be of the spreading type, thus giving homozygous erect offspring.

In the cross of Golden Eyed Wax with Prolific Black, outstretched branches due only to axial inflorescence were noted.

Spreading plants of this nature also occur in the cross of Bountiful and Prolific Black Wax. In the latter two crosses the twining habit was more or less developed in the longer branches.

CROSS TYPE 34, 35, OR 36. $alt \times alt$, $alt \times alt$, OR
 $alt \times alt$

In the crosses of this type only erect bush beans without runners or spreading branches, should occur, although contorted stems might possibly appear. Such is the behavior of the following crosses of this type:

Low Champion \times Blue Pod Butter

Blue Pod Butter \times Golden Eyed Wax and reciprocal

Blue Pod Butter \times Mohawk and reciprocal

Challenge Black Wax \times Warwick

Currie \times Mohawk and reciprocal

Currie \times Red Valentine

Blue Pod Butter \times Warren

Bountiful \times German Black Wax

In the crosses, Challenge Black Wax by Davis Wax and Blue Pod Butter by Davis Wax, lots have been isolated with short shoots above the plants somewhat resembling the habit of Burpee Stringless and Giant Stringless. This behavior is unexpected if such a plant type is to be described by the formula ALT. The Davis Wax type used in the crosses may, however, have been of a different strain from that described in the table. This variety is the only one used in the crosses that was not under the observation of the writer, as its growth was discontinued the year in which these notes were taken.

While the factors discussed above primarily determine the plant habit, there are several others of secondary consideration. No special notes were taken with regard to

these. Some of them are mentioned in the following paragraph.

The character of the habit type is somewhat influenced by the amount of branching the plants exhibit; open, loose, bush beans are the result of few branches; the close, dense habit of some forms is caused by profuse branching. The size of a plant to some extent influences the habit, although not as much in small ones like Challenge Black Wax. In Warren the size of the plant probably causes it to droop. In some varieties the number and weight of the pods, as well as their position, cause some plants to droop and assume a spreading habit when old. Perhaps fineness and coarseness of branching affect habit.

One further matter that comes up for consideration is the question of the effect of environment upon plant habit. Its greatest effect, as would be supposed, seems to be upon such quantitative characters as length of the plant axis and probably the twining character to some extent. Instances of adverse conditions resulting in the almost total suppression of a character were noted in plants grown on poor soil. They exhibited the slender tips, typical of vines with axial inflorescence, but were otherwise bush-like and erect. The accelerating effects of very fertile soil on the growth of runner was also noted. However, the environmental explanation for the sudden appearance of runners among bush beans or of pole beans among typical runners is open to question. The most probable cause of such phenomena lies primarily in the regrouping of the unit characters of habit, combined at times with checking and accelerating factors external to the plant.

The investigations here reported offer a foundation upon which more extensive study on the subject might be based.

The following table suggests a few important cross types and the varieties which might be used to advantage:

CROSSES FOR FURTHER STUDY

No.	Type Number	Varieties		Plant Type
1	2	Golden Carmine	× White Marrow and reciprocal	$a \times b$
2	3	Golden Carmine	× Burpee Stringless and reciprocal	$a \times c$
3	4	Golden Carmine	× Refugee and reciprocal	$a \times d$
4	5 or 6	Golden Carmine	× Keeney and reciprocal	$a \times e$
5	7 or 8	Golden Carmine	× Challenge Black and reciprocal	$a \times f$
6	10	White Marrow	× Burpee Stringless and reciprocal	$b \times c$
7	11	White Marrow	× Refugee and reciprocal	$b \times d$
8	12 or 13	White Marrow	× Keeney and reciprocal	$b \times e$
9	14 or 15	White Marrow	× Challenge Black and reciprocal	$b \times f$
10	17	Burpee Stringless	× Refugee and reciprocal	$c \times d$
11	18 or 19	Burpee Stringless	× Keeney and reciprocal	$c \times e$
12	20 or 21	Burpee Stringless	× Challenge Black and reciprocal	$c \times f$
13	23 or 24	Refugee	× Keeney and reciprocal	$d \times e$
14	25 or 26	Refugee	× Challenge Black and reciprocal	$d \times f$
15	29 or 30	Keeney	× Challenge Black and reciprocal	$e \times f$

The Burpee crosses should be particularly watched to determine if the assumed set of factors AIT is the cause of the shoots and later spreading habit of the plant.

The axis should be studied by means of accurate measurement as far as possible. The judgment concerning circumnutation would probably be necessarily more or less indefinite.

In crosses 4, 5, 8, 9, 11, etc. the type number should be determined.

The conclusions that can be drawn from observations reported in the preceding pages are:

1. That plant habit in beans is largely determined by the presence or absence of three characters which have been designated by the letters A, L, and T.

1. A, the presence of axial inflorescence permitting an indefinite growth, of the main stem and main branches, and a terminal inflorescence causing definite growth.

2. The length of the axis L, an important factor controlling plant habit and probably governed by a series of two or more factors for a length L_1 , L_2 , etc., which behave after the fashion of Emerson's hypothesis for the inheritance of quantitative characters.

3. The climbing habit is due to a factor for circum-

mutation. This factor may be called T. The cause of the various degrees of the climbing habit has not been determined with any degree of certainty. The contorted stems of erect bush forms are probably caused by T.

II. The factors A, L and T may be present in any possible combination, giving rise to the various habit types of beans.

III. When the types are crossed among themselves they behave approximately after the manner sketched in Table II.

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